

EARLY PLIOCENE GREBES, BUTTON-QUAIL, AND
KINGFISHERS FROM SOUTH-WESTERN CAPE PROVINCE,
SOUTH AFRICA
(AVES: PODICIPEDIDAE, TURNICIDAE, HALCYONIDAE)

By

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(With 3 figures and 1 table)

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ABSTRACT

Two species of grebes (Podicipedidae) occur sparingly among the abundant fossil remains of birds found in the early Pliocene Varswater Formation at Langebaanweg, south-western Cape Province. The most abundant of these is a small species that is indistinguishable from the modern dabchick *Tachybaptus ruficollis*, which ranges from South Africa through Eurasia, as far as New Guinea. In their smaller size, these fossils agree with the African subspecies *T. r. capensis*, as opposed to larger forms in Europe and Asia, and appear to indicate a 5-million-year period of stasis in this lineage in southern Africa. The second species of grebe is much rarer, being known from three bones only. These are robust and superficially most similar to the New World genus *Podilymbus*, but are sufficiently different to be tentatively referred to the widespread genus *Podiceps*. These fossils represent a new, extinct lineage of grebes for Africa.

A single fossil of a button-quail is most similar to the living species *Turnix hottentotta* and provides the first Tertiary occurrence of the family Turnicidae.

Three bones of kingfishers are referable to a species of *Halcyon* similar in size to *H. albiventris*, and to a species of *Ceryle* about the size of the New World *C. alcyon*, which represents a size-class of *Ceryle* that is now extinct in Africa.

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INTRODUCTION

The deposits of the early Pliocene Varswater Formation near Langebaanweg, Cape Province, have yielded one of the largest Tertiary avifaunas yet discovered (Rich 1980; Hendey 1981*a*, 1981*b*, 1982). The elucidation of this vast amount of material continues slowly, with the avian taxa treated so far including the Procellariiformes (Olson 1985*a*), Scopidae (Olson 1984), Plataleidae (Olson 1985*c*), Ciconiidae (Haarhoff 1988), Rostratulidae (Olson & Eller 1989), and Coliidae (Rich & Haarhoff 1985).

The three families covered in the present report have little in common other than the uncertain ordinal affinities of the first two. The grebes (Podicipedidae) are usually accorded their own order Podicipediformes, placed near the loons (Gaviiformes), but are probably most closely related to families included in the Gruiformes (Olson 1985*b*), whereas the button-quails (Turnicidae), which have traditionally been placed in the Gruiformes, actually have no close relatives within that varied assemblage (Olson & Steadman 1981).

Fossils from Langebaanweg are from the collections of the Department of Cenozoic Palaeontology, South African Museum, Cape Town, and are prefixed SAM-PQ, which has generally been omitted below.

Comparative material examined

Material of Podicipedidae included skeletons representing all living species except *Podiceps pelzelni* of Madagascar (see list in Olson in press). Material of *Tachybaptus ruficollis* included the subspecies *T. r. ruficollis* (1 female from Germany, USNM); *T. r. poggei* (5 males and 7 females from China, USNM); *T. r. capensis* (1 male from Zimbabwe, USNM; 1 female from South Africa, USNM; and an unsexed specimen each from Gabon, FMNH, and Tanganyika, UMMZ); *T. r. philippensis* (1 male from Luzon, USNM); and *T. r. tricolor* (1 female from Celebes, USNM). Of African Turnicidae, 3 skeletons of *Turnix sylvatica lepurana* (USNM 429078, 429079, 430658) and 1 skeleton of *T. hottentotta nana* (CM 1160) were examined. Representative skeletons of each of the species of Halcyonidae mentioned were all from the USNM collections.

SYSTEMATICS

Order 'PODICIPEDIFORMES'

Family Podicipedidae

Only three species of grebes occur in Africa today, all of which are widespread Palaearctic forms. The lack of endemism among African grebes contrasts rather markedly with South America or even Australia. Because none of the modern African grebes have differentiated at the specific level within Africa, it becomes of interest to determine when each of the species may have become established in the continent. Although the grebes are osteologically more homogeneous than reflected by modern generic usage, I have followed the nomenclature of Storer (1979).

Genus *Tachybaptus* Reichenbach, 1853*Tachybaptus ruficollis* (Pallas, 1764)

Fig. 1

Material

Coracoid: complete right—L53324; complete left—L22417D, L50050E; right scapular end—L25514BC. Humerus: proximal right—L22755, L50342E, L56221B; proximal left—L22941, L50069A, L55048, L56221A; distal right—L42745H, L50582J, L55049, L56222B; distal left—L56222A, L56222C. Carpometacarpus: left proximal—L17060B, L34956, L34957. Femur: complete right—L50056A; complete left—L22422K, L50056B, L53322; proximal left—L42853G; distal right—L50012WV, L53323. Tibiotarsus: right lacking proximal end—L56220B; left lacking proximal end—L56220A, L61672, L22450Q; distal right—L23646, L24125N; distal left—L22422AA, L25601LF, L25602EN, L50048G, L50379F; juv.—L42854G; juv.—L50048J. Tarsometatarsus: complete left—L57854, L50063B; proximal right—L25292E, L25293EC, L50012AG, L50062E; proximal left—L28423DV, L50577AG, L50577R; distal right—L50062F1, L50062F2, L50577W; distal left—L17006F, L50577AL, L50577N; lacking inner trochlea—L22420I.

The total number of specimens is 56 and, if each site in the mine is considered separately, the minimum number of individuals involved would be 16.

Measurements

See Table 1.

Stratigraphic provenance

Early Pliocene, Varswater Formation: Quartzose Sand Member (18 specimens, minimum number of individuals 7); Pelletal Phosphorite Member Bed 3aN (36 specimens, minimum number of individuals 8); Pelletal Phosphorite Member Bed 3aS (3 specimens, minimum number of individuals 1).

Remarks

Despite a good sample from Langebaanweg, including highly diagnostic elements, I was unable to distinguish any differences whatever between the fossils and the living dabchick *Tachybaptus ruficollis*. Furthermore, although the comparative sample sizes were small in some cases, the measurements of the fossils are consistently small, and thus appear to conform to the size of the small African subspecies *T. r. capensis*, as opposed to the larger European and Asian races (Table 1). This implies an extraordinary period of stasis of some 5 million years (Hendey 1981: 95) within this species' lineage in southern Africa. It might also imply that the size differences associated with subspecific differentiation may have originated millions of years ago in this lineage. On the other hand, it is equally possible that the smaller size is primitive and that the larger size of more northern forms was derived subsequent to the early Pliocene. Regardless, the dabchick seems to have been in South Africa for at least 5 million years, during which it shows no osteological changes.

TABLE 1

Comparison of fossils from Langebaanweg referred to *Tachybaptus ruficollis* with modern specimens of the African subspecies *T. r. capensis* and the Asian subspecies *T. r. poggei*. (Measurements following in parentheses are from a single specimen each of *T. r. ruficollis*, *T. r. philippensis*, and *T. r. tricolor*, respectively.)

Measurement	n	Range	Mean	Population
CORACOID				
Greatest length	2	22.5-22.7	22.6	<i>T. r. capensis</i>
	3	21.0-22.6	21.8	fossils
	12	22.6-26.9	24.7 (25.7, 25.2, 23.1)	<i>T. r. poggei</i>
HUMERUS				
Proximal width	3	8.3-9.0	8.7	<i>T. r. capensis</i>
	6	8.2-9.6	8.8	fossils
	12	8.9-10.2	9.5 (10.4, 9.7, 9.4)	<i>T. r. poggei</i>
Distal width	4	5.2-5.5	5.3	<i>T. r. capensis</i>
	6	4.8-5.4	5.2	fossils
	12	5.3-6.1	5.7 (5.8, 5.7, 5.9)	<i>T. r. poggei</i>
CARPOMETACARPUS				
Proximal depth	4	4.6-4.8	4.7	<i>T. r. capensis</i>
	3	4.7-4.8	4.7	fossils
	12	4.5-5.1	4.9 (5.3, 5.2, 5.0)	<i>T. r. poggei</i>
FEMUR				
Length	3	27.7-29.2	28.3	<i>T. r. capensis</i>
	4	25.2-27.4	26.5	fossils
	12	27.9-31.3	29.6 (31.4, 31.4, 28.6)	<i>T. r. poggei</i>
Proximal width	4	6.5-7.3	6.8	<i>T. r. capensis</i>
	5	6.3-7.3	6.7	fossils
	12	7.0-7.8	7.4 (7.4, 7.7, 7.8)	<i>T. r. poggei</i>
Distal width	4	6.7-7.4	7.1	<i>T. r. capensis</i>
	7	6.0-7.4	6.6	fossils
	11	7.3-8.4	7.8 (7.6, 7.7, 7.8)	<i>T. r. poggei</i>
TIBIOTARSUS				
Distal width	4	5.2-5.7	5.4	<i>T. r. capensis</i>
	13	5.0-6.0	5.3	fossils
	12	5.4-6.2	5.9 (5.8, 6.0, 6.0)	<i>T. r. poggei</i>
TARSOMETATARSUS				
Length	4	33.1-34.8	33.8	<i>T. r. capensis</i>
	2	33.1-32.7	32.9	fossils
	12	33.1-37.4	35.1 (38.6, 38.7, 35.7)	<i>T. r. poggei</i>
Proximal width	4	5.6-6.2	6.0	<i>T. r. capensis</i>
	8	5.4-6.0	5.7	fossils
	12	5.8-7.1	6.5 (6.6, 6.5, 6.5)	<i>T. r. poggei</i>
Width trochleae 3, 4	4	4.1-4.8	4.5	<i>T. r. capensis</i>
	9	4.2-4.7	4.4	fossils
	12	4.4-5.3	4.9 (5.2, 5.1, 5.2)	<i>T. r. poggei</i>

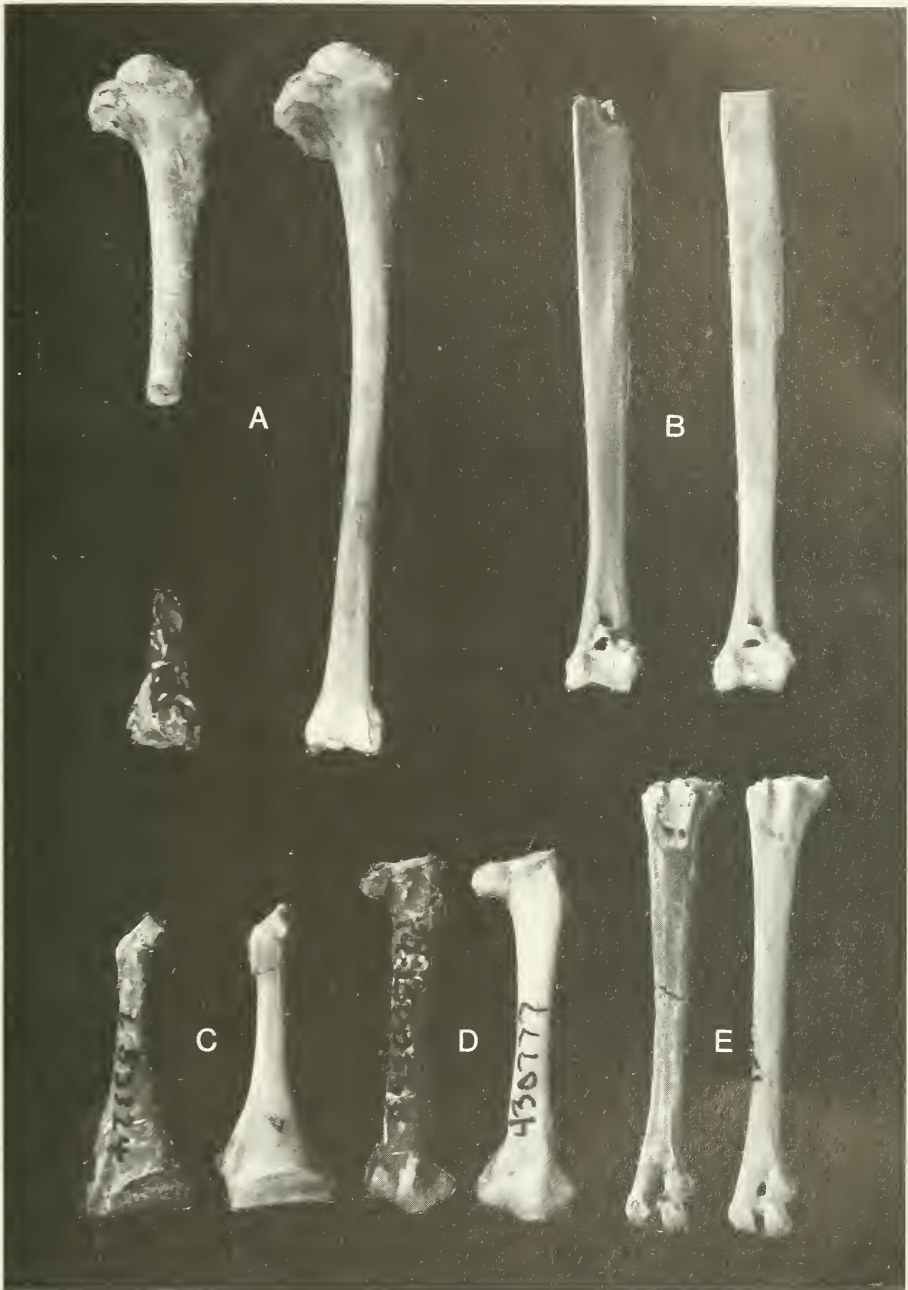


Fig. 1. Fossils of *Tachybaptus ruficollis* from Langebaanweg compared to a modern specimen of the same species (USNM 430777—on the right in each pair). A. Humeri in anconal view (proximal end—L50342E; distal end—L50582J). B. Tibiotarsi in anterior view (L61672). C. Coracoids in ventral view (L53324). D. Femora in anterior view (L50056B). E. Tarsometatarsi in posterior view (L57854). All figures $\times 1.8$.

The dabchick in southern Africa is mainly confined to still or slow-moving bodies of fresh water, usually with emergent vegetation. It invariably nests in such situations, but non-breeders may occur rarely in marine environments on the west coast (Maclean 1985). The greater number of specimens and individuals in the Pelletal Phosphorite Member (PPM) of the Varswater Formation is probably a reflection of the fluvatile origins of those deposits, as opposed to the more estuarine or marine environments of the Quartzose Sand Member.

Genus *Podiceps* Latham, 1787

Podiceps? sp.

Fig. 2

Material

Humerus: complete right—L50069; distal left—L46678C. Tarsometatarsus: distal right—L50352E.

The total number of specimens is three and the minimum number of individuals is one.

Measurements (in mm)

Humerus: length, 72.2; proximal width, 12.3; distal width, 7.3, 7.8. Tarsometatarsus: distal width through inner and outer trochleae, 5.9.

Stratigraphic provenance

Early Pliocene, Varswater Formation: all three specimens are from the Pelletal Phosphorite Member Bed 3aN.

Remarks

These three bones are from a grebe quite unlike any hitherto known from Africa, being much too small for *Podiceps cristatus*, and larger and much more robust than either *P. nigricollis* or *Tachybaptus ruficollis*. Brodkorb (1985) reported fossils of a medium-sized grebe from the Upper Pliocene and Lower Pleistocene Beds I and II of Olduvai, Tanzania. I compared Brodkorb's material directly with the fossils from Langebaanweg and found that two very different species were represented, with the Olduvai bird being considerably smaller and more gracile, and thus more like *P. nigricollis*.

The length of the single complete humerus from Langebaanweg is near the maximum for *P. nigricollis* or the minimum for *P. auritus*, and falls well within the range of the New World pied-billed grebe *Podilymbus podiceps* (see Storer 1976). The relative robustness of the shaft is greater than in any of those species and the width of the distal end of the other humeral specimen exceeds that of any of the 38 specimens of *P. podiceps* measured by Storer (1976). In the complete specimen, the scar for M. scapulohumeralis anterior is very deep, although this tends to be somewhat variable individually in modern grebes.



Fig. 2. Fossils of *Podiceps?* sp. from Langebaanweg compared with *Podilymbus podiceps* and *Podiceps nigricollis gurneyi* (USNM 558364). Right humeri in anconal view ($\times 1.5$). A. *P. podiceps* (USNM 500858). B. *Podiceps?* sp., L50069. C. *Podiceps?* sp., L46678C. D. *P. nigricollis*. Right tarsometatarsi in posterior view. ($\times 2$); E. *P. podiceps* (USNM 610577). F. *Podiceps?* sp., L50352E. G. *P. nigricollis*.

The tarsometatarsus of the fossil is much more robust than in modern species of *Podiceps* of comparable size and is superficially similar to *Podilymbus*. It differs from *Podilymbus* in having trochlea II situated farther distally, and trochlea IV extending distally to about the same extent as trochlea III, rather than being more proximal as in *Podilymbus*. The fossil is evidently less specialized than modern species of *Podiceps* of roughly comparable size (e.g. *P. auritus* or *P. nigricollis*) in having the shaft less laterally compressed and trochlea II less retracted proximally and medially, but is not too unlike certain smaller taxa such as *P. occipitalis*. It differs from any of these species in having the distal foramen smaller.

The general resemblance of these fossils is closest to that of *Podilymbus*, a genus that is altogether unknown in the Old World. On the other hand, the differences between *Podilymbus* and *Podiceps*, in the skeletal elements represented as fossils, are not particularly trenchant, so that given the age of the fossils one could not be certain that these three bones are not from a very robust, perhaps highly localized endemic form of *Podiceps* with a circumscribed range, such as *Podiceps gallardoi* of Southern Argentina is today. Another possibility is that the rarity of this species at Langebaanweg may indicate that it was only a casual wanderer to the area.

Whatever the generic relationships or the previous distribution of this enigmatic grebe may have been, it definitely represents a lineage of Podicipedidae hitherto unknown in Africa. We can only hope that more diagnostic material, such as a femur—which in *Podilymbus* is much longer and more gracile than in other grebes—will surface and help to clear up taxonomic uncertainties.

Order 'GRUIFORMES'

Family Turnicidae

Genus *Turnix* Bonnaterre, 1791

Turnix cf. *T. hottentotta* Temminck, 1815

Fig. 3B

Material

Humerus: distal right—L43366A.

The total number of specimens and minimum number of individuals is one.

Measurements (in mm)

Humerus: distal width, 4.0.

Stratigraphic provenance

Early Pliocene, Varswater Formation: Pelletal Phosphorite Member Bed 3aS or possibly the Quartzose Sand Member (Dump 7).

Remarks

This specimen is one that I encountered among some unsorted avian material, the family Turnicidae not having previously been noted at Langebaanweg (Rich 1980; Hendeby 1981*b*). The skeleton in the Turnicidae presents a mosaic of unique characters and those of several other orders. It is not unlikely, therefore, that more material of *Turnix* is included among the fossils referred to the Rallidae, Phasianidae, or even Charadriiformes. The apparent scarcity of button-quails at Langebaanweg is thus to some extent probably an artefact.

The fossil was compared with the two African species of *Turnix* but, as only one specimen was available anywhere for *T. hottentotta*, the results are inconclusive. The bone from Langebaanweg seems to be more like *T. hottentotta* in having the ectepicondylar process more robust and laterally (as opposed to proximally) oriented. It differs from either of the modern species in having the proximal end of the radial condyle sharply demarcated from the shaft.

Turnix hottentotta is the only button-quail in the western Cape Province today. It prefers short, moist grasslands, in contrast to *T. sylvatica*, which occurs in ranker grasses (Snow 1978). If the fossil is correctly associated with the *T. hottentotta* lineage, it would accord well with the inferred environmental conditions at Langebaanweg in the early Pliocene (Hendeby 1981*b*; Olson 1985*c*).

Order CORACIIFORMES

In her preliminary account, Rich (1980) indicated the presence of the order Coraciiformes at Langebaanweg. Based on her identifications, Hendeby (1981*b*) listed one species of Coraciiformes of undetermined family and at least two species of kingfisher (Alcedinidae = Halcyonidae), neither identified to genus. The amount of coraciiform material in the collections from Langebaanweg is very scant and, in looking over the few fossils that had previously been assigned to this group, I found that the majority had been misidentified to order. When the bones of falcons, doves, and parrots had been removed, only three specimens remained. These represent two species in two genera of kingfishers, no other taxa of Coraciiformes (or Bucerotiformes) as yet being indicated. The material at present is insufficient for the characterization of new species, although it is likely that more fossils of kingfishers will become available with further sorting of the Langebaanweg collections.

Family Halcyonidae

Genus *Halcyon* Swainson, 1821

Halcyon sp.

Fig. 3D

Material

Tibiotarsus: distal right—L24593H.

The total number of specimens and minimum number of individuals is one.

Measurements (mm)

Tibiotarsus: distal width, 3.2.

Stratigraphic provenance

Early Pliocene, Varswater Formation: Quartzose Sand Member.



Fig. 3. Button-quail and kingfishers from Langebaanweg. A-C. Distal ends of right humeri of *Turnix* in palmar view ($\times 3$). A. *Turnix hottentotta nana* (CM 1160). B. Fossil *Turnix* cf. *T. hottentotta* (L43366A). C. *Turnix sylvatica lepurana* (USNM 429079). D-F. Leg elements of kingfishers ($\times 4$). D. Distal end of right tibiotarsus of *Halcyon* sp. (L24593H), anterior view. E. Distal end of left tibiotarsus of *Ceryle* sp. (L24001JR), anterior view. F. Distal end of right tarsometatarsus of *Ceryle* sp. (L24000FL), posterior view.

Remarks

This specimen is referable to *Halcyon*, as contrasted to *Ceryle*, by the constricted shaft proximal to the condyles, especially noticeable on the posterior face; also the markedly narrower medial condyle and wider tendinal bridge. In *Alcedo*, the lateral condyle is much narrower and the tendinal bridge is smaller than in the fossil. The specimen is from a species about the size of *H. albiventris*. The living African species of *Halcyon* are, for the most part, inhabitants of open savanna and bushlands, but occur in nearly every ecotype other than desert. No species of *Halcyon* occurs in the Langebaanweg area today, the nearest approach being made by *H. albiventris*, which extends along the south-eastern coast of South Africa to the vicinity of Cape Town.

Genus *Ceryle* Boie, 1828

Ceryle sp.

Fig. 3E-F

Material

Tibiotarsus: distal left—L24001JR. Tarsometatarsus: right, lacking proximal end and inner and outer trochleae—L24000FL.

The total number of specimens is two and the minimum number of individuals is one.

Measurements (mm)

Tibiotarsus: distal width, 3.8. Tarsometatarsus: no meaningful measurements possible.

Stratigraphic provenance

Early Pliocene, Varswater Formation: Quartzose Sand Member.

Remarks

The tarsometatarsus in the ceryline kingfishers differs greatly from that in *Halcyon* in being markedly shorter and stouter. The fossil tarsometatarsus from Langebaanweg agrees with *Ceryle* in these respects but differs from any of the species examined in having the scar for the hallux more deeply excavated, creating much more of an indentation in the medial margin of the bone. Also, the distal foramen is more proximally situated.

The tibiotarsus is from a species much larger than the preceding species of *Halcyon*, and possesses the characters of *Ceryle* as outlined above, although it has a wider tendinal bridge than in living forms of that genus. It would appear to be from a species similar in size to that represented by the tarsometatarsus, and both are tentatively referred to the same species.

This kingfisher was considerably larger than *C. rudis* but much smaller than *C. maxima*, and would more closely have approximated the size of the New World species *C. alcyon* or *Chloroceryle amazona*. The proportions of the tarsometatarsus are intermediate between the very short, stout bone of *Ceryle*

alcyon and the more elongate tarsometatarsus in *Chloroceryle amazona*. The two fossils from Langebaanweg are clearly from an undescribed, extinct species of *Ceryle* belonging to a size-class that is now absent from Africa. The living species of *Ceryle* are all piscivorous and hence are almost invariably found near water. Both of the extant species in South Africa (*C. rudis* and *C. maxima*) also frequent the seashore and coastal lagoons, in addition to freshwater streams and lakes.

DISCUSSION

The inferred habitat requirements of the grebes, button-quails and kingfishers from Langebaanweg are in agreement with environmental reconstructions based on a variety of data, including other taxa of birds, and indicate a stream in rather open savanna. As with other groups of birds, the present selection consists of species that are almost certainly on a direct line to existing species, as well as species belonging to lineages that have become entirely extinct. The *Tachybaptus* at Langebaanweg, which is represented by a considerable number of specimens, cannot be distinguished from the existing species *T. ruficollis*. The button-quail (*Turnix*) and one of the kingfishers (*Halcyon*) are too poorly known to be certain of their specific relationships but are not very different from living taxa, whereas the remaining grebe (*Podiceps*) and kingfisher (*Ceryle*) belong to size-classes within their respective genera that have vanished from Africa since the Pliocene.

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